

THE ROLE OF THE FUNGUS *CENOCOCCUM GRANIFORME* (SOW.) FERD. ET WINGE IN THE FORMATION OF MOR

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WHAT FACTORS REGULATE THE FORMATION OF MOR?

The mor profile is characterized by the accumulation of decaying plant debris on the mineral soil (Kubiena, 1953). This results, a.o., from the low activity of micro-organisms. Humus respiration, that is, the consumption of oxygen per gramme of organic material, is a measure of the intensity of decomposing organic material by fungi and bacteria. Under *Fagus sylvatica* in the upper fermentation layer of mor, it reaches 3/4 of the mull-value, while in the humus layer it attains only 1/4 of the mull-value (Meyer, 1959).

The low microbial activity is closely related to the many factors which account for the formation of mor, such as:

(a) Unfavourable properties of litter. For example: an ample C/N-ratio (Wittich, 1943); a high lignin content (Grosskopf, 1928); a low number of bases (Wittich, 1952) (Laatsch, 1957), and a high tannin content, which precipitates proteins and thus renders them resistant to attack (Handley, 1954).

(b) Disadvantageous soil properties: poverty of bases and nutrients, sand with low water capacity, close texture and checked ventilation.

(c) Climatic factors: a cool and rainy climate (Hesselman, 1925); low temperatures hamper the microbial activity and high rainfalls favour eluvation of nutrients.

(d) Economic measures play a role in the vegetation influenced by man. Only the upper layers of soil are included in the circle of nutrients in a stand of planted trees with shallow rooting, whereas nutrients illuviated into the deeper layers are lost to the circle of nutrients (Hartmann, 1961). Soil temperature is decreased in a stand with a dense canopy in comparison to an open stand, as is microbial activity.

THE OCCURRENCE OF HYPHAE OF *CENOCOCCUM* IN MOR

Besides the factors mentioned under (a)–(d) the fungus *Cenococcum graniforme* plays a particular role in the formation of mor. Lihnell (1942) advocates aligning *Cenococcum graniforme* in the ascomycetes, since the structure of the wall of their sclerotia resembles the perithecium wall of the ascomycetous genus *Cephalotheca*. *Cenococcum graniforme* is capable of existing saprophytically, as well as in symbiosis with trees. Among the mycorrhizal fungi, *Cenococcum graniforme* shows the widest host range

(Trappe, 1962); it is a symbiotic partner of nearly all the trees in the forests of the boreal and temperate zones. The hyphae of *Cenococcum graniforme* are characterized by thick walls and a blackish-brown colour, and their diameter generally varies between 4–6 μ . It occurs in all forest soils, but in an abundant quantity in mor. The fungus does not seem to form a mycorrhiza with *Calluna*, so the following statements are only valid for forest humus.

P.E. Müller, the father of humus micromorphology, observed a great deal of blackish-brown mycelium in mor of Danish beech forests as early as 1887. Based on our present knowledge, the mycelium mentioned by Müller (1887) might belong to the fungus *Cenococcum graniforme*. Before the role of this fungus in the formation of mor is discussed, its ecology should be briefly described.

THE RESISTANCE OF CENOCOCCUM AGAINST DROUGHT

Investigations of the ecology of *Cenococcum graniforme* were initiated in the autumn of 1959, when the influence of summer drought on mycorrhizas was studied in the surroundings of Hamburg. During the examination it was found that in soils which had suffered greatly from the drought the quantity of *Cenococcum* mycorrhizas had increased in contrast to those with hyaline hyphae. It could be noticed repeatedly that hyphae of *Cenococcum graniforme* established themselves on the surface of light-coloured mycorrhizas, the cortex tissue of which was entirely shrunk under the influence of drought, whereas mycorrhizas still intact were free of blackish-brown mycelium (Fig. 1). *Cenococcum graniforme*, therefore, seems to possess a higher resistance to drought than other mycorrhizal fungi.

Witkamp (1960) reports that his counts of mycelium in soil in November 1959 (soil suspension slide method) gave a percentage value of 91–100% thick and brown mycelia.

In order to study the influence of water supply on the occurrence of *Cenococcum graniforme*, the following experiment was conducted: Young plants of *Fagus sylvatica* were cultivated in a green-house in earthenware pots filled with different humus forms (mull, moder and mor), and watered as follows: series A received water every time that it was necessary, series B received water one half as often as A, series C received water one third as often as series A, and series D received water one fourth as often as series A. The result of this experiment is shown in Table I.

It can be seen from Table I that *Cenococcum graniforme* behaves towards increasing soil drought in a different manner than other mycorrhizal fungi. While the share of the latter is reduced strongly, the percentage of *Cenococcum* mycorrhiza remains either unchanged, or even slightly greater (in moder). The differential sensitiveness of mycorrhizas to water deficiency results in the relative enrichment of *Cenococcum graniforme* during drought. Similar results were obtained by Worley and Hacskeylo (1959).

Table I further indicates that *Cenococcum graniforme* is also present in mull, although not in the same amount as in mor. Here too there is a relative enrichment of *Cenococcum* with increasing drought. Since *Cenococcum graniforme* plays a minor role in mull under natural conditions, the water economy might be more balanced in mull than in mor.

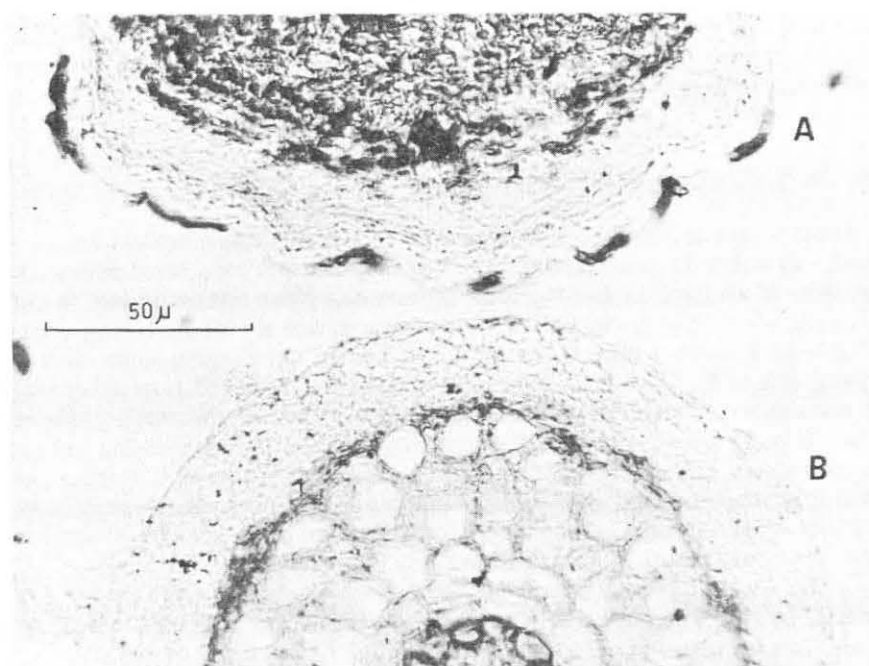


Fig.1.A. Mycorrhiza that had suffered under the drought of the summer 1959. The tissue of the cortex is shrunken and in the fungus sheath *Cenococcum graniforme* has established itself. B. Intact mycorrhiza without colonization of *Cenococcum graniforme*.

TABLE I

Influence of different moisture content of soil on the development of mycorrhizas of two-year-old beech seedlings (cultivated in the humus layer). The numbers indicate the percentage of root tips converted into mycorrhizas.

	Mull		Moder		Mor	
Watering	<i>Ceno-</i> <i>coccum</i> <i>graniforme</i> mycorrhiza	Other mycor- rhizas	<i>Ceno-</i> <i>coccum</i> <i>graniforme</i> mycorrhiza	Other mycor- rhizas	<i>Ceno-</i> <i>coccum</i> <i>graniforme</i> mycorrhiza	Other mycor- rhizas
every time	5	75	15	60	30	40
every 2nd time	5	55	15	35	30	20
every 3rd time	5	30	20	10	30	10
every 4th time	5	30	20	5	30	5

As shown in Table I the water factor has a decisive significance in the distribution of *Cenococcum*. Hence in the following paragraphs the water economy of mor will be compared with that of mull. The occurrence of mycorrhizal fungi is determined less by average values of water content in humus than by extreme values. This is especially true for periods of dryness lasting for only a short time; even a short period of dryness may kill the tender hyphae of many mycorrhizal fungi. An extreme period of drought may change the fungus flora of tree roots to a great degree; *Cenococcum*

graniforme, being more resistant to drought, then gets the upper hand and the roots harbouring it may only be very slowly recolonized by the other mycorrhizal fungi.

THE WATER ECONOMY OF MOR

In order to get an idea of which layers of the different humus forms the supply of water is most endangered during the periods of drought, the intensity of rooting in the various layers has been investigated in detail. The intensity of rooting in the different layers gives a hint as to the capability of trees to absorb water from these layers in correspondence with their rooting intensity. The root tips of *Fagus* are converted into mycorrhizas to a great extent, which facilitates the uptake of water; in those parts of the root distal to the root tip the water uptake decreases by increasing suberization of root cortex (Kramer, 1956). Therefore the number of root tips per unit of volume was counted in the different layers of soil. In respect to the capacity of water uptake, the number of root tips ecologically gives a better scale of measurement than the length or the weight of the roots.

The intensity with which *Fagus sylvatica* roots in the diverse horizons of mull, moder and mor soils is shown in Fig.2 (concerning the properties of the sample plots cf. Meyer, 1959, 1962). From Fig.2 it follows that the intensity of rooting in the different humus forms is rather different. In mull, *Fagus sylvatica* develops a maximum of 556 root tips per 100 ml of soil (H2). In mor, on the contrary, 45,600 root tips (upper F3) develop. This extraordinarily great difference in the intensity of rooting results, among others, from the nutrient supply of the soil. According to the findings of Kern et al. (1961), the total length of tender roots is closely related to the nutrient content of the soil: "The higher the available supply of nutrients, the less is the amount of tender roots necessary for its exploitation".

However, not only does the number of root tips show considerable deviations between the different humus forms, but the distribution of roots in the different layers does too. As Fig.2 shows, in the eutrophic brown earth the roots are spread in nearly the same manner in all the layers; in the podsol brown earth there is a tendency to prefer the fermentation-layer, while in podsol nearly all tender roots occur in the fermentation-layer, and the layers beneath are only weakly or not at all traversed by roots. In the mineral soil of podsol the nutrient supply is so low that the roots first develop in the A-horizon, where nutrients become available to plants in the course of decomposition of litter. This concentration of roots near the surface leads to quick exhaustion of water in A-horizon in drought periods, while in eutrophic brown earth all soil layers are utilized to nearly the same degree.

CAUSES FOR THE ABUNDANCE OF *CENOCOCCUM* IN MOR

Fig.2 shows, furthermore, that the share of *Cenococcum graniforme* increases with the rooting intensity. The highest number of *Cenococcum graniforme* mycorrhizas occurs in the F3 layer of mor (podsol), which is

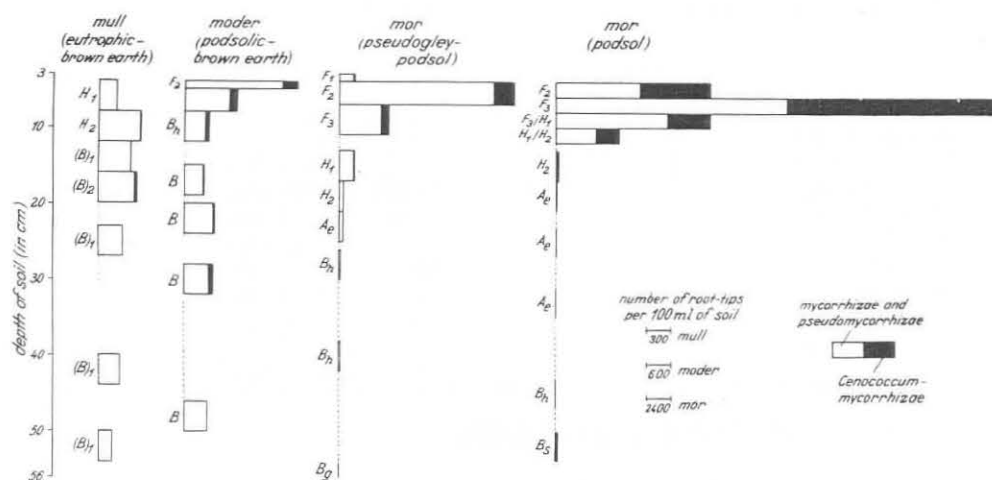


Fig.2. Intensity of rooting of *Fagus sylvatica* in various layers of eutrophic brown earth, podsolic-brown earth, pseudogley-podsol and podsol. Nomenclature of soils and soil horizons according to Kubiena (1953).

most intensely interwoven by roots. This enormous development of *Cenococcum* might particularly be traced back to the unbalanced water economy in the strongly rooted layers. Besides this, the resistance capacity of *Cenococcum graniforme* to certain antibiotics may play a role, for in mor antibiotics are produced by fungi in larger quantities (Brian, 1949). For example, Levisohn and Parry (1960) found that the development of many mycorrhizal fungi is inhibited by antibiotics formed by *Alternaria tenuis*; only *Boletus subtomentosus* and *Cenococcum graniforme* (= *Mycelium radialis nigrostrigosum*) were not influenced by these substances.

Not only do the mycelia of *Cenococcum* occur in great quantities in mor, but the black-coloured sclerotia do too. Sclerotia are to be found in mull and moder as well, but in smaller quantities and as small-sized ones. The sclerotia are predominantly formed in such layers where the conditions of existence become more disadvantageous to *Cenococcum graniforme*, viz. in the zone of transition between the humus-rich upper soil and the humus-poor mineral soil. The thin sections of this zone are characterized by numerous sclerotia. The distribution of the sclerotia in the different layers of podsol is shown in Table II.

From the preceding paragraphs it follows that the abundance of *Cenococcum graniforme* in mor must be traced back to the concentration of roots in the A-horizon in the first place. This fact, characteristic of mor, implies that the water content of mor decreases to a high degree in drought periods, and this facilitates the relatively better growth of *Cenococcum graniforme*.

TABLE II

Distribution of sclerotia of *Cenococcum graniforme* in the podsol profile.

Mor/Pseudogley-Podsol		Mor/Podsol	
Layer	Number of sclerotia per 100 ml of soil	Layer	Number of sclerotia per 100 ml of soil
F1 (3- 4 cm)	0	F2 (4- 6 cm)	0
F2 (4- 7 cm)	1	F3 (6- 8 cm)	8
F3 (7-11 cm)	2	F3/H1 (8-10 cm)	35
H1 (13-17 cm)	14	H1/H2 (10-12 cm)	89
H2 (17-21 cm)	251	H2 (13-17 cm)	161
Ae (21-25 cm)	16	Ae (17-21 cm)	203
Bh (26-30 cm)	9	Ae (23-27 cm)	134
Bh (38-42 cm)	2	Ae (31-35 cm)	51
Bg (54-58 cm)	0	Bh (43-47 cm)	47
		Bs (50-54 cm)	75

CENOCOCCUM IN THIN SECTIONS OF MOR

The observation of thin sections shows that the blackish-brown hyphae of *Cenococcum* contribute to a great deal of the material of mor, especially in the lower fermentation and the upper humus layers, the numerous hyphae of *Cenococcum* are a characteristic feature of thin sections of mor, (cf. Plate A4 and A5). *Cenococcum* does occur in the B-horizon too (Plate A6).

The enrichment of the dark hyphae is not only favoured by periodic drought, but also by the fact that they undergo decomposition more slowly than the tender hyaline hyphae. Martin et al. (1959) investigated the disintegration of 25 microscopic fungi and found that the light-coloured hyphae are destroyed more quickly than the darker ones. The investigation of thin sections also supports the opinion of a slow decomposition of *Cenococcum* hyphae. For we see that after the death of *Cenococcum graniforme* mycorrhizas the decay of root tissue proceeds at a rapid rate, while the mycelia of the fungal sheath are still visible in the form of dark rings; later these rings disintegrate into pieces. A further reference to the difficult decomposability of the *Cenococcum* hyphae is furnished by the data on humus respiration (Meyer, 1959). In the upper fermentation layer of mor (podsol) the litter of beech is attacked with an intensity of 78% of that of mull, whereas in the humus layer of mor, with its high content of *Cenococcum* hyphae, the rate of decomposition amounts to only 24% of that of mull. Thus, the "permanent humus" of mull is more intensively decomposed than the material of the H-layer of mor.

In the lower part of the humus layer a great many fragments of dark hyphae are conspicuous, the contours of which often appear blurred in thin sections. This may be a hint that a slow decomposition of dark hyphae takes place here or that the hyphae undergo autolysis (cf. Plate A4).

DISCUSSION

The findings of the present investigation appear to contribute an important factor to the problem of mor formation. No doubt poverty of bases in soil and the other previously mentioned factors play a decisive role in mor formation. However, mor formation is not only the result of a slow decay of litter. As seen above, in the course of litter decomposition there is an intensive production of dark hyphae, which are apparently more difficult to decompose than the litter itself. Consequently, the lower part of the A-horizon of mor not only consists of the organic material derived from litter, but new organic material has been added to such a degree that the properties of the humus layer are considerably changed.

In mor the organic litter material is not only enriched by dark hyphae during its decomposition, but an enrichment of other organic materials, neither included in the litter nor derived from it, also takes place (namely that of rootlets). To what degree the great quantities of roots influence the chemical composition of certain layers may be shown by the values of C/N-ratio as given by Meyer (1959). In the mull with poor root contents, the C/N-ratio gradually decreases during litter decay. In the mor it first decreases, and there rises again in the intensively rooted layers (F3 and H1). This increase might be partly traced back to the additional organic material of the roots.

The concentration of roots near the surface of the soil is important for the development of *Cenococcum graniforme*. In podsol this shallow rooting is determined by a deficiency of nutrients. In addition, in pseudogley-podsol the rooting is impeded in subsoil through unfavourable texture and low oxygen content. Though the properties of förna and upper fermentation layer (pH-value, N-content, number of bacteria) in the pseudogley-podsol plot resemble those of moder or partly even those of mull, mor formation takes place, and the humus layers of pseudogley-podsol and podsol exhibit the same feature by the dominance of hyphae of *Cenococcum graniforme*.

The fungus *Cenococcum graniforme* seems to be widely distributed. It was found by various authors in humus forms characterized by periodic drought or nutrient deficiency. Thus Mikola and Laiho (1962) report that *Cenococcum* is a typical mycorrhizal fungus in Finnish spruce forests which especially occurs in the surface layers. Göbl (cited in Schiechl and Stern, 1963) found in samples taken from *Abies cilicica*-dry forests of Taurus predominantly black mycorrhizae, which resemble those that are formed by *Cenococcum graniforme*. According to Wright (1963) *Cenococcum graniforme* is favoured by the low moisture content of soil in central Oregon.

SUMMARY

The mycelia of *Cenococcum graniforme* play an important role both quantitatively and qualitatively in mor, and exhibit a significant micromorphological feature in the humus layer of mor. The intensive development of *Cenococcum graniforme* in mor is promoted a.o. by periodic drought which is caused by the concentration of roots in the upper layers of podsol. The accumulation of roots in the A-horizon of mor is again a consequence of the deficiency of nutrients or oxygen in the subsoil.

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COLOURED ILLUSTRATIONS

Plate A4. Thin section of humus layer (H2) of pseudogley-podsol. The humus layer contains many hyphae and fragments of hyphae. Some of the fragments appear blurred. In the centre of the figure the remains of a *Cenococcum graniforme* fungal sheath is visible; x 300.

Plate A5. Humus layer of mor. *Cenococcum graniforme*-mycorrhiza, the decay of which is in progress. The root tissue has been decomposed and the fungal sheath has not yet been disintegrated; x 300.

Plate A6. *Cenococcum graniforme*-mycorrhizae in the Bh-horizon of podsol. Crossed nicols.

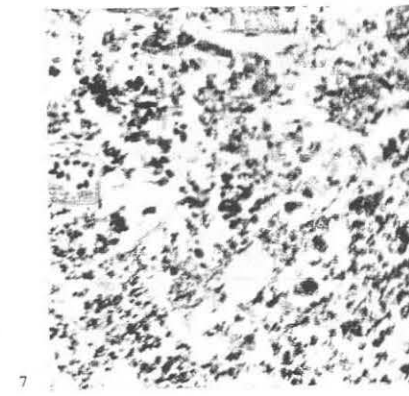
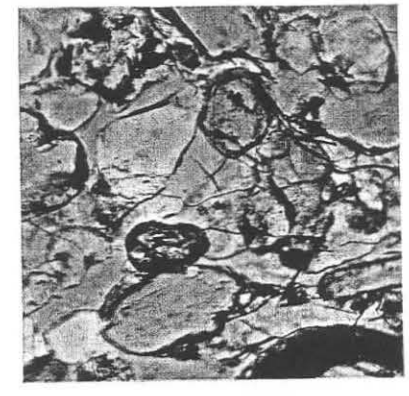
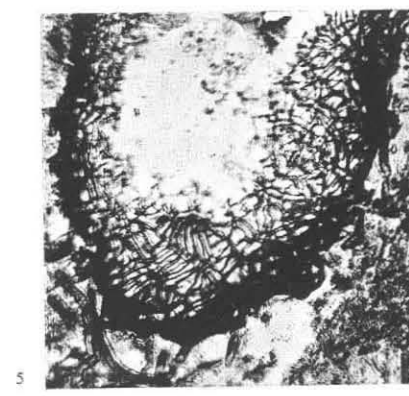
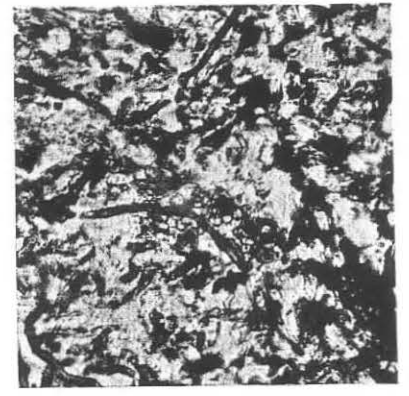
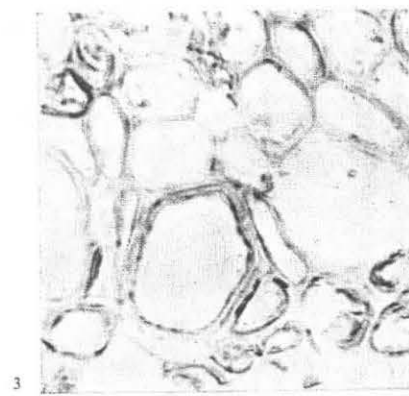
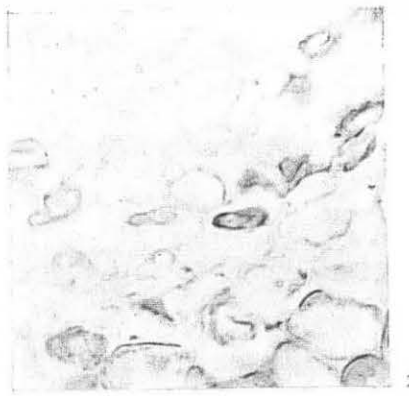
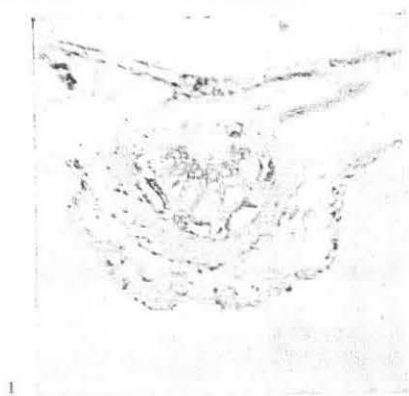


PLATE A